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Elevational patterns and determinants of plant diversity in the Baekdudaegan Mountains, South Korea: Species vs. functional diversity

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The elevational gradient present in mountainous areas provides the most powerful natural experimental system available to clarify the ecological and evolutionary responses of living organisms to geophysical influences. In this study, we explored the elevational patterns of plant species and functional diversity and the effects of area, mid-domain effect, climatic variables and net primary productivity on the observed diversity patterns along the ridge of the Baekdudaegan Mountains, South Korea. Rapoport's elevational rule was also evaluated by examining the relationship between elevational range size of plant species and elevation. A total of 802 plant species from 97 families and 342 genera were found in 1100 plots along a 200- –1900-m elevational gradient along the ridge. The elevational patterns of plant species diversity along the ridge of the Baekdudaegan depicted distinctly hump-shaped patterns, whereas the functional diversity decreased monotonically with elevation. The mid-domain effect was the most powerful explanatory variable for species diversity patterns. However, climatic variables were better predictors for functional diversity. Moreover, Rapoport's elevational rule was not supported. Our study suggests that different elevational patterns may be observed among different diversity measurements even in the same taxon and that there may be fundamental differences in the mechanisms underlying these diversity patterns.

climatic variables, elevational gradient, functional diversity, mid-domain effect, species diversity

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Mountain ranges generally support biologically diverse communities with a high proportion of endemic species and harbor most of the world's protected areas [1,2]. The biodiversity in mountain ecosystems and their geographical distribution have received considerable interest from ecologists and biogeographers over the last decade because understanding biodiversity patterns is important for biodiversity conservation, sustainable use and natural reserve area planning and management [3]. The elevational gradient present in mountainous areas provides the most powerful natural experimental system available to clarify the ecological and evolutionary responses of living organisms to geophysical influences [4]. Many studies have documented the elevational diversity patterns of plants, mammals, birds, and invertebrates and different patterns have been observed in different taxa and regions [5–8]. There are three main types of diversity patterns in relation to increasing elevation: (1) a monotonic decrease; (2) a plateau at low elevations; and (3) a "hump-shaped" distribution with high diversity at intermediate elevations [9]. Of these three main types of elevational patterns, the hump-shaped pattern is recognized as the most common type.

Although the mechanisms underlying elevational diversity patterns are still subject to debate, typical explanations include the influence of variables such as climate, area, mid-domain effect or geometric constraints, productivity

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and evolutionary history [7] and Rapoport's elevational rule [10]. Climate is considered to be the most widely supported predictor of worldwide biodiversity because climate can directly control species distributions when climatic conditions exceed the physiological tolerances of species and can indirectly affect photosynthetic activity and biological processes. Several studies have also found that the area of elevational bands explained a large proportion of the variation in diversity [6,11], similarly to the well-known species-area relationships. Recent studies have suggested the mid-domain effect (MDE), or geometric constraints, is highly effective at explaining elevational diversity patterns [7,12]. The MDE postulates that geometric constraints on species ranges within a bounded domain will yield a mid-domain peak in diversity regardless of ecological factors [13]. Productivity is another variable that can influence biodiversity patterns. Although the relationship between diversity and productivity has been very controversial, with disagreement over whether productivity controls or is controlled by diversity [14], productivity is frequently cited as a fundamental determinant of diversity [15]. Rapoport's elevational rule suggests that climates at higher elevations are more variable, so species at higher elevations must be able to tolerate a broad range of climatic conditions and therefore have larger elevational ranges. Consequently, species diversity is inflated at low elevations and the diversity decreases with elevation [10].

Many investigators have documented and agreed that biodiversity plays a pivotal role in various aspects of ecosystem functioning such as productivity, stability and resilience, and perhaps biodiversity reduces invisibility, with evidence explored by both theoretical and experimental approaches [16,17]. Although biodiversity has been defined as the variety of life forms at all levels of biological organization including taxonomic, genetic, phenetic and phylogenetic diversity [18], species diversity has long been recognized and used as the single most important component and measure of biodiversity in many studies [19]. Moreover, species diversity has been also used as the main index in most studies linking biodiversity to ecosystem functioning [20], but the link between species diversity and ecosystem functioning has been highly controversial [21]. A variety of experiments performed in different ecosystems have revealed that increased species diversity is positively related to improved ecosystem functioning [14,22]. However, other studies have found no or negative relationships between these two variables [22,23]. Thus, although an overall effect of species diversity on ecosystem functioning often exists, the relationship is not always predictable and the cause of this variation among studies remains unclear [24].

In recent years, traditional biodiversity indices, such as species richness and diversity, have been supplemented or replaced by functional diversity, which is used to measure those components of biodiversity that influence how an ecosystem operates or functions [25]. Functional diversity is defined as the extent of functional differences among the species in a community or ecosystem and is often used to describe several different aspects of community or ecosystem structure, such as the variation in the functional traits [26]. Several studies report that species and functional diversity must be considered simultaneously to allow the identification of the effects of various mechanisms within biodiversity ecosystem functioning [24–27].

Although many studies have looked at species and functional diversity in mountain ecosystems, few studies have comprehensively analyzed and used those different diversity indices and there is still little evidence showing how species and functional diversity vary across environmental gradients in forests. Moreover, despite the growing attention given to changes in diversity patterns with elevation recently, few studies have analyzed the functional diversity patterns and the underlying mechanisms along elevational gradients [28,29].

In this context, we examined species and functional diversity patterns of terrestrial plants along an elevational gradient on the ridge of the Baekdudaegan Mountains (hereinafter referred to as "the Baekdudaegan"), South Korea. Using field surveys of plant data, the objective of the present study was: (1) to explore and compare the elevational patterns of species and functional diversity; (2) to evaluate the effects of area, the MDE, mean annual temperature and precipitation and an enhanced vegetation index as a proxy of above ground net primary productivity on the elevational patterns of species and functional diversity; and finally (3) to examine the relationship between elevational range size of plant species and elevation to test Rapoport's elevational rule.

1 Material and methods

1.1 Study area

The study area covered the main ridge of the Baekdudaegan (35°15′–38°22′, 127°28′–129°3′E) in South Korea (Figure 1). The Baekdudaegan consists of about 487 mountains, hills, and peaks along the Korean peninsula and serve as a major resource for forest biodiversity [30]. The Korea Forest Service designated the protected area of the Baekdudaegan in September 2005; the total protected area, including the main ridge, covers 2634 km^2 (1712 km^2 core area and 922 km^2 buffer zone). The main ridge extends about 650 km from Hyangnobong Peak (1287 m above sea level, a.s.l.) to Mt. Jiri (1917 m a.s.l.) in South Korea, where one can travel along the ridgeline without crossing any rivers or streams. The elevational gradient of the main ridge extends from 200 to 1909 m a.s.l. based on a digital elevation model (DEM) generated using a mosaic of 1:25000 scale topographical maps covering the study area produced by the National Geographic Information Institute (Figure 1(a)).

The Baekdudaegan in South Korea belongs to a moun-

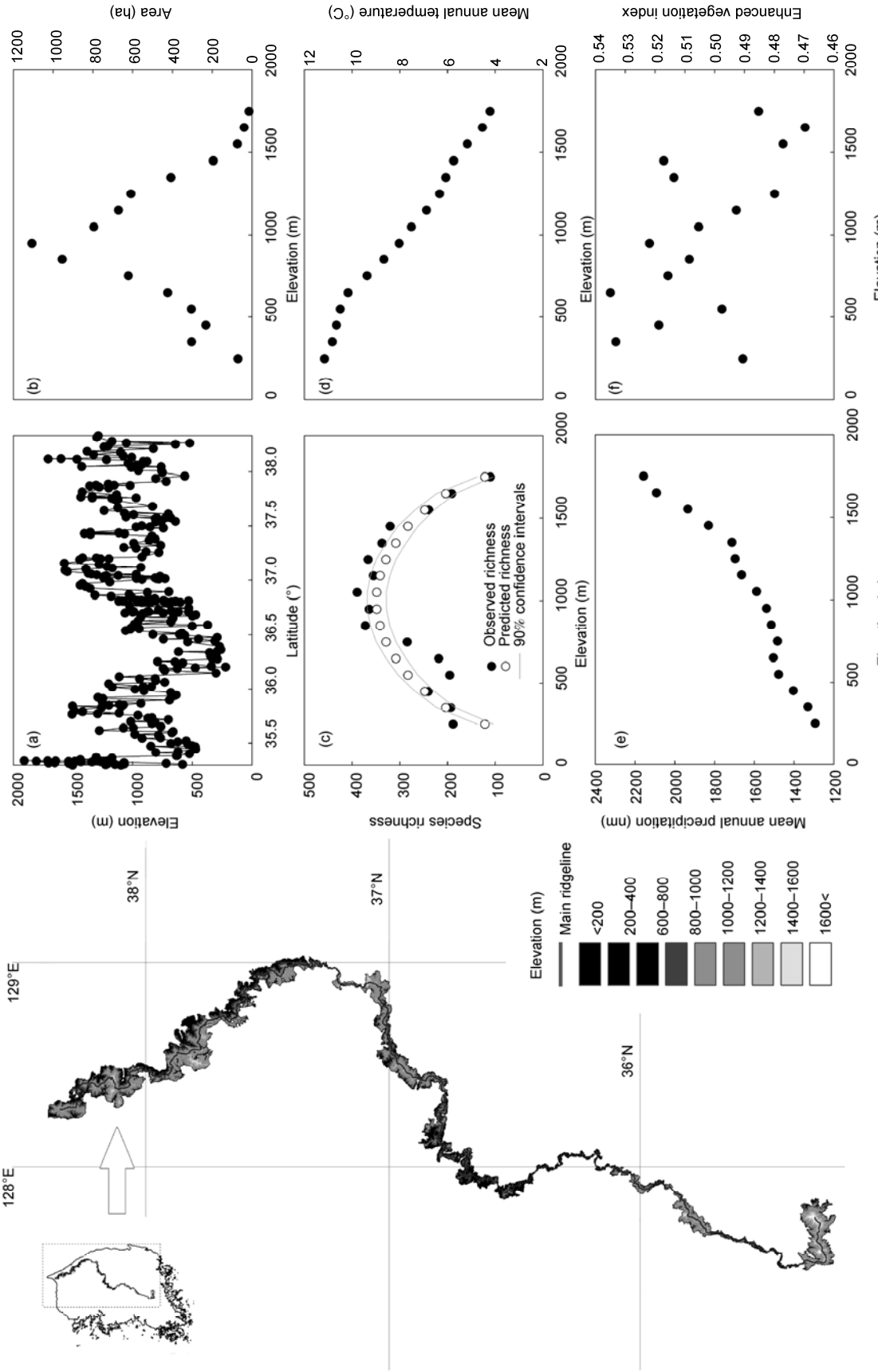

Figure 1 Location, topography and explanatory variables of the study area, the ridge of the Baekdudaegan Mountains in South Korea. Relationships between elevation and (a) latitude, (b) area, (c) mid-domain effect (MDE), (d) mean annual temperature (MAT), (e) mean annual precipitation (MAP) and (f) enhanced vegetation index (EVI). Area, MAT, MAP and EVI were calculated for each elevational band in an imaginary 100-m-wide transect along the ridge of the Baekdudaegan. The predicted MDE richness and 95% confidence intervals were computed from 5000 randomizations with MDE null model.

tainous ecoregion and temperate deciduous and mixed forest biome [30]. The soil consists of granite, granite gneiss, and highly deformed and recrystallized sedimentary rocks [31]. The Baekdudaegan has many biodiversity hotspots and offers natural habitats for an abundant and varied fauna and flora even though the natural environment of the Baekdudaegan remains poorly known because insufficient survey data exist. The Korea Forest Research Institute reported a total of 1477 plant species occurred along the Baekdudaegan, accounting for 35.2% of the vascular plant diversity on the Korean peninsula [30].

The vegetation on the Baekdudaegan can be categorized into 49 communities, including seven cultivated communities (e.g., the *Larix kaempferi* community) and 42 natural vegetation communities (e.g., the *Quercus mongolica* community). The Korea Forest Research Institute divided the Baekdudaegan in South Korea into three parts based on characterized plant community groups: (1) the northern part, characterized by *Acer komarovii* and *Betula ermanii*, (2) the central part, characterized by *Acer pseudosieboldianum* and *Fraxinus rhynchophylla*; and (3) the southern part, characterized by *Abies koreana* and *Fraxinus mandshurica* [30]. The vegetation on the Baekdudaegan can also be divided into four major zones along an elevational gradient. These elevational vegetation zones include: (1) temperate (montane) deciduous broad-leaved and pine forest (< 550 m a.s.l.) dominated by *Pinus densiflora* and *Rhus tricocarpa*; (2) temperate deciduous broad-leaved and coniferous mixed forest (550–1100 m a.s.l.) dominated by *Q. mongolica*, *Quercus serrata*, *Pinus koraiensis*, and *Abies holophylla*; (3) sub-alpine coniferous forest (1100–1600 m a.s.l.) dominated by *Taxus cuspidata*, *A. koreana*, and *Abies nephrolepis*, and (4) alpine forest (> 1600 m a.s.l.) dominated by *B. ermanii* and *Pinus pumila* [32].

1.2 Plant data and diversity indices

To carry out field sampling, an imaginary 100-m-wide transect was made in a north-south direction along the ridge of the Baekdudaegan, and the ridge was divided into 16 elevational bands at 100-m intervals from 200 m a.s.l. to more than 1700 m a.s.l.. Although the sampling covered up to approximately 1900 m, areas with elevations exceeding 1700 m were considered as a single band because only a small number of plots were sampled and a small number of plant species were observed in this elevational band. Plant data were collected within every elevational band of this 100-m-wide transect from May 2005 to August 2009. Vegetation sampling was performed to determine the most common and specific physiognomic vegetation types in each 100 m elevational band. The data were obtained from a total of 1100 plots of 400 m^2. Within each plot, plants were surveyed based on the Braun-Blanquet method [33]. Table S1 lists the plant species and life form checklists at each elevational band.

To examine the relationships between plant diversity and elevation, the data from the sampled plots within each elevational band were pooled, and species and functional diversity indices were calculated based on incidence and weighted by species frequencies within each elevational band. We used two species diversity indices. First, species richness was defined as the number of species in each elevational band. Second, the Shannon-Wiener index (H') as a measurement of species diversity is traditionally calculated as

$$H' = -\sum_{i=1}^{S} p_i \ln p_i , \quad (1)$$

where S and p_i are the number of species (i.e., species richness) and the proportion of the ith species in an elevational band. In addition to species diversity indices, we also calculated functional diversity (*FD*). To calculate functional diversity, we classified plant species into nine life forms according to Raunkiaer's system [34]; megaphanerophytes, microphanerophytes, nanophanerophytes, therophytes, geophytes, hemicryptophytes, chamaephytes, as well as helophytes and hydrophytes as a single group and epiphytes. Functional diversity is based on the adaptation of an index of species dissimilarity [35]

$$FD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j , \quad (2)$$

where d_{ij} is the dissimilarity (i.e., not necessarily a metric distance) between species i and j. The relative abundances of p_i and p_j represent the ith and jth species in an elevational band. The parameter d_{ij} can vary from 0 (when two species belong to exactly the same functional group) to 1 (when two species belong to completely different functional groups). In the case of data for categorical functional groups such as our study, when two species belong to the same functional group (i.e., ith and jth species are megaphanerophytes), then $d_{ij} = 0$; when each pair of species belongs to different functional groups (i.e., ith species and jth species are a megaphanerophyte and a microphanerophyte, respectively), then $d_{ij} = 1$. Therefore, the functional diversity is the sum of the dissimilarity in trait space among all possible pairs of species, weighted by the product of the species' relative abundance. Based on this procedure, first, we calculated the dissimilarity among all pairs of species and relative abundance of each species was calculated in each elevational band. Finally, functional diversity in each elevational band was calculated through the summation of dissimilarities weighted by species' relative abundances. Functional diversity was computed with an Excel macro available at http://botanika.bf.jcu.cz/suspa/FunctDiv.php [36].

Moreover, the rarefaction approach was performed to rectify the bias caused by different sample sizes among elevational bands. All diversity indices were rarefied at the lowest number of samples (n = 26) observed at the 1700 m

elevational band. Rarefied diversity indices allow us to compare the diversity indices along the elevational gradients using an equal number of samples for each elevational band.

Unlike many recent studies, we did not use interpolated diversity indices modified from actual distribution records. Interpolation is often used to compensate for gaps in elevational distribution caused by undersampling [12]. However, several studies have reported three problems with interpolation [3,12,37]. First, it disrupts the crucial control of sampling area and intensity as species are added that were not in fact present in the plots. Second, interpolation might artificially increase species richness at intermediate elevations, because gaps are filled only between the lower and upper range limits; this basically assumes that no individuals of a species have been missed beyond the observed range limits, but that individuals have been missed at sampling points within the range limits. Third, diversity indices at nearby elevations are more similar than at distant elevations, and the resulting spatial autocorrelation inflates Type I errors. The spurious effects of autocorrelation increase when using interpolated distributional data. However, many studies on elevational diversity patterns have used interpolated data, so comparisons of such studies with our non-interpolated results might be difficult. Therefore, we also calculated interpolated diversity indices. Observed and interpolated diversity indices were strongly correlated (species richness, R^2 = 0.92; species diversity, R^2 = 0.90; functional diversity, R^2 = 0.93; $P < 0.001$ in all cases) and these results indicate the same patterns exist in both observed and interpolated indices along the elevational gradient. Thus, we presented results based only on the observed values without interpolation in this study.

1.3 Explanatory variables

Two spatial-related variables, area and MDE, were investigated with respect to the diversity indices. To test species-area relationships, we calculated the area of each elevational band along the 100 m wide transect. Calculations were performed using a digital elevation model (DEM) with 1 arc-second resolution with the DEM Surface Tools extension in ArcGIS 9.3. The DEM Surface Tools can derive surface area from slope and aspect within a cell using Berry's method [38] calculating an adjustment factor based on precalculated slope for the cell planimetric area. The area can be calculated as

$$\text{Area} = \frac{c^2}{\cos\left(S\left(\frac{\pi}{180}\right)\right)}, \tag{3}$$

where c and S indicate the cell size in each elevational band and slope in degrees for each cell, respectively.

The MDE null model was used to test the influence of geometric constraints on the spatial patterns of species richness along an elevational gradient. We used a novel, discrete MDE model based on Colwell and Hurtt's continuous Model 2 [39], which does not necessitate the use of interpolated ranges [40]. In this model, sampling points along the domain are treated as ordered, evenly spaced, discrete bins. A species' range is measured as the number of bins between the highest and the lowest elevational bands at which that species occurs, including those extreme bands, regardless of how many occupied elevational bands or unoccupied elevational bands occur within the range. Occupancy is measured as the total numbers of bands at which a species occurs, including the extreme bands that define its range. The objective of the null model is to generate the pattern of species richness over the ordered bins (the domain) that would be expected if observed species' ranges were placed at random within the domain, maintaining their observed range sizes and occupancies, under the geometric constraint that no range may extend beyond the domain limits. The ordered bins that represent the domain are indexed by the integers $1 \cdots Q$. Each species' range is systematically selected, one species at a time (without replacement), then placed independently and at random on the discrete domain. This process begins by choosing a (uniform) random digit between 1 and Q to represent the potential midpoint of the chosen range. If the range lies fully within the domain, given its size and this random midpoint, the range is kept in that position. Initially, a successfully placed range occupies all intervening bins between its range endpoints, but occupancy is immediately adjusted to the recorded occupancy for that species by deleting, at random, as many occurrences as necessary from the interior of the range. The algorithm then repeats with the next species' range [41]. RangeModel software version 5 was used for simulation [42]. The simulation process was repeated 5000 times and we used expected mean richness and its 95% confidence intervals to assess the effects of geometric constraints on the elevational gradient.

The two climatic variables used in this study are mean annual temperature (MAT) and precipitation (MAP). We used digital climate maps produced by the Korea Meteorological Administration and National Center of Agrometeorology to extract the meteorological parameters for each elevational band [43]. MAT data were dated from 1971 to 2008, and MAP data were dated from 1981 to 2009. The spatial resolution of the raster data was 30 m for MAT and 270 m for MAP. MAT and MAP were calculated for each elevational band in the 100 m wide transect along the ridge of the Baekdudaegan.

As a proxy for above-ground net primary productivity, we used the enhanced vegetation index (EVI), which has been preferred over the Normalized Difference Vegetation Index because it is not sensitive to soil or atmospheric effects and adjusts the red wavelength as a function of the blue wavelength to minimize brightness-related soil effects

[44]. MODIS-driven EVI images, composited at 16-day intervals, were downloaded in tiles for the period between January 2004 and December 2009 and mosaicked together using the MODIS re-projection tool. The averaged annual EVIs were used to assess the relationship between the diversity indices and productivity.

1.4 Rapoport's elevational rule

To examine the relationship between the elevational range size of plant species and elevation, the elevational range size of plant species was quantified by calculating (1) the mean range size of all the species present in an elevational band (Stevens' method) [10] and (2) the range size only of species whose range midpoints are in a particular band (midpoint method) [45]. The relationship between elevational range size of plant species and elevation was evaluated using simple regression analysis. When the relationship between both variables is positive, Rapoport's elevational rule is predicted to hold true.

1.5 Statistical analysis

The relationships between diversity indices and the explanatory variables were calculated for each individual variable using a simple linear regression. Such a linear model tests only for linear relationships between the potential explanatory variables and diversity indices, but there are several plausible scenarios under which a unimodal model is actually more biological reasonable [12]. Therefore, we also examined a polynomial regression model to detect such curvilinear relationships, including a quadratic term in the regression function. Finally, we used forward stepwise multiple regression models to establish the relative importance of area, MDE, MAT, MAP and EVI as explanatory variables of species and functional diversity indices. Forward stepwise multiple regressions are used here to find a set of independent variables that together provide the best fit for diversity indices by minimizing the sum of squared residuals. However, because area and MDE have hump-shaped elevational patterns (Figure 1(b) and (c)) and thus they are collinear with each other, we used the variation partitioning approach with removing or including MDE in multiple regression models to disentangle the independent effects between area and MDE. All linear and quadratic terms of the explanatory variables were used in forward stepwise multiple regression. Simple and forward stepwise multiple regression models were performed with S-PLUS version 8.0.

2 Results

2.1 General description

With increasing elevation, the area of the elevational bands increased steeply, and then decreased after reaching 900–1000 m, showing a hump-shaped pattern (Figure 1(b)). The MDE null model showed deviation of the observed species richness from simulated richness (Figure 1(c)). The analysis revealed that 50% of the data points fell outside the 95% confidence interval of the MDE null model for overall species richness. MATs declined monotonically with increasing elevation (Figure 1(d)), whereas MAPs increased along the elevational gradient (Figure 1(e)). EVIs generally declined with increasing elevation (Figure 1(f)).

A total of 802 plant species belonging to 97 families and 342 genera were recorded from 1100 plots along the elevational gradient on the Baekdudaegan (Tables 1 and S1). More than half of these species were herbaceous (69%; 62

Table 1 Observed and rarefied diversity indices for different elevational bands along the ridge of the Baekdudaegan Mountains, South Korea

Elevational band (m)	No. of plots	Species richness		Species diversity		Functional diversity	
		Observed	Rarefied	Observed	Rarefied	Observed	Rarefied
200	36	188	168	4.837	4.781	0.810	0.810
300	64	193	137	4.623	4.480	0.808	0.807
400	64	240	167	4.831	4.682	0.811	0.811
500	46	195	153	4.698	4.595	0.813	0.812
600	61	218	152	4.759	4.596	0.807	0.805
700	93	284	174	4.946	4.751	0.807	0.806
800	117	372	201	5.113	4.890	0.804	0.804
900	113	364	198	5.124	4.861	0.808	0.807
1000	103	389	218	5.197	4.957	0.801	0.800
1100	72	355	231	5.257	5.051	0.796	0.796
1200	70	366	239	5.231	5.050	0.798	0.797
1300	68	337	224	5.156	4.986	0.794	0.792
1400	75	320	212	5.088	4.919	0.798	0.797
1500	54	239	178	4.801	4.679	0.804	0.804
1600	38	191	159	4.610	4.541	0.811	0.810
1700	26	110	110	4.227	4.227	0.797	0.798
All bands pooled	1100	802	659	5.478	5.542	0.809	0.815

families, 249 genera, and 554 species), while woody species account for 31% (47 families, 99 genera, and 248 species). In relative proportions of functional groups, megaphanerophytes (22.6%), geophytes (22.3%) and hemicryptophytes (21.6%) were the dominant life forms on the ridge of the Baekdudaegan (Figure 2(a)). Megaphanerophytes, nanophanerophytes and therophytes showed decreasing patterns with elevation ($R^2 > 0.67$, $P < 0.001$ in all cases), whereas hemicryptophytes, microphanerophytes, as well as the helophytes and hydrophytes as a group and the epiphytes showed increasing patterns with elevation ($R^2 > 0.40$, $P < 0.01$ in all cases). Geophytes ($R^2 = 0.60$, $P = 0.002$) and chamaephytes ($R^2 = 0.17$, $P = 0.112$) showed hump-shaped pattern and no relationship with elevation, respectively (Figure 2(b)–(e)).

2.2 Elevational diversity patterns with explanatory variables

In elevational plant diversity patterns, observed species richness peaked in the elevational band between 1000 and 1100 m, whereas rarefied richness had the peak between 1200 and 1300 m (Figure 3(a) and (b)) with both peaking in the elevational band between 1100 and 1200 m for species diversity (Figure 3(c) and (d)). Overall, both species richness and diversity showed hump-shaped patterns even though the absolute elevations of the peaks were different somewhat between the two indices. However, functional diversity monotonically decreased with elevation (Figure 3(e) and (f)).

Based on simple linear regressions, species richness and diversity were strongly correlated with the MDE and area, whereas MAT was a significant predictor for functional diversity (Linear model in Table 2). However, the results from the quadratic models were somewhat different from those of the simple linear models. The MDE, area and climatic variables were significant predictors of plant species richness and diversity, whereas climatic variables, MAT and MAP were still powerful predictors for functional diversity (quadratic model in Table 2).

The forward stepwise multiple regression models with all linear terms of explanatory variables included only the MDE and explained 74% and 64% of the variations in species richness and diversity, respectively (Model A in Table 3). A second model (Model B in Table 3), excluding the MDE, included only the area and explained 65% and 49% of the variations in species richness and diversity, respectively. The model including the MDE has higher explanatory power than the model excluding the MDE. However, climatic variables such as MAT and MAP were powerful predictors regardless of MDE and explained 61% of the variation in functional diversity patterns on the ridge of the Baekdudaegan. Moreover, the results with all linear and quadratic terms of explanatory variables were also similar to those with only linear terms of the variables. Overall, the MDE was the most powerful variable to explain elevational species richness and diversity patterns, whereas climatic variables were better predictors for functional diversity

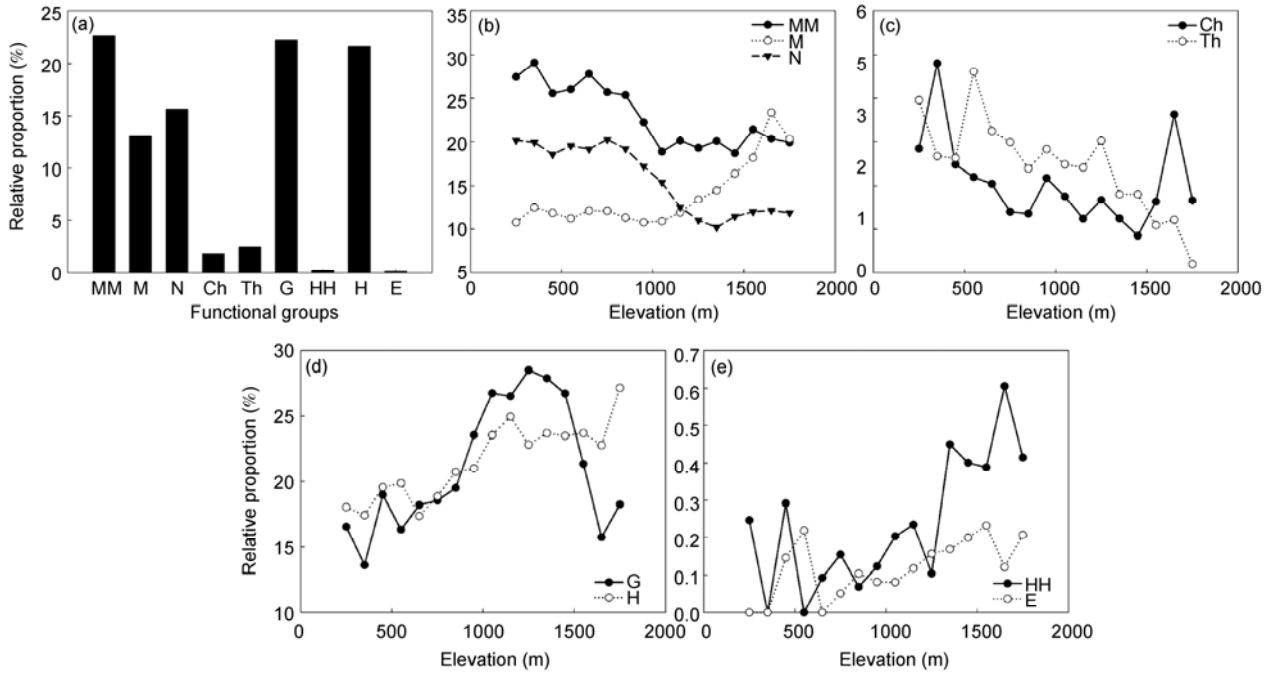

Figure 2 Changes in the relative proportions of different functional groups on the ridge of the Baekdudaegan. (a) Overall, (b)–(e) elevational changes among functional groups. Functional groups were classified into nine life forms according to Raunkiaer's system (1934): megaphanerophytes (MM), microphanerophytes (M), nanophanerophytes (N), therophytes (Th), geophytes (G), hemicryptophytes (H), chamaephytes (Ch), helophytes and hydrophytes (HH) and epiphytes (E).

Table 2 Simple linear and quadratic models for explained variables and diversity indices along the ridge of the Baekdudaegan, South Korea

Diversity index	Variable	Linear model			Quadratic model		
		F	R^2	P	F	R^2	P
Species richness	Area	25.87	0.65	< 0.001	13.64	0.68	< 0.001
	MDE	39.21	0.74	< 0.001	23.78	0.79	< 0.001
	MAT	0.18	0.01	0.676	67.5	0.91	< 0.001
	MAP	0.44	0.03	0.516	17.8	0.73	< 0.001
	EVI	0.41	0.03	0.534	1.68	0.21	0.224
Species diversity	Area	13.19	0.49	0.003	8.37	0.56	0.005
	MDE	24.35	0.64	< 0.001	12.89	0.67	< 0.001
	MAT	< 0.01	< 0.01	0.981	24.67	0.79	< 0.001
	MAP	1.35	0.09	0.265	20.81	0.76	< 0.001
	EVI	0.32	0.02	0.579	1.75	0.21	0.213
Functional diversity	Area	0.26	0.02	0.618	0.51	0.07	0.611
	MDE	0.92	0.06	0.354	1.09	0.14	0.364
	MAT	9.06	0.39	0.009	7.13	0.52	0.008
	MAP	3.39	0.20	0.087	4.78	0.42	0.028
	EVI	0.21	0.02	0.653	0.7	0.1	0.515

a) Magnitudes of F-values indicate the importance of each variable in the models. MDE, mid-domain effect; MAT, mean annual temperature; MAP, mean annual precipitation; EVI, enhanced vegetation index.

pattern on the ridge of the Baekdudaegan.

2.3 Rapoport's elevational rule

Although the relationships between elevational range size of plant species and elevation were different between Stevens' (Figure 4(a)) and the midpoint (Figure 4(b)) methods, simple linear regression analysis between elevational range size and elevation showed no significant positive relationships on the ridge of the Baekdudaegan. Therefore, these analyses do not support Rapoport's elevational rule.

3 Discussion

In this study, we explored plant species and functional diversity patterns along an elevational gradient and the underlying mechanisms using primary data at a regional scale on the ridge of the Baekdudaegan, South Korea. The elevational diversity patterns and their underlying causes have long been controversial issues in ecology and biogeography [12]. Moreover, few studies have analyzed how functional diversity varies along elevational gradients and what kind of variables control the elevational functional diversity pattern [28]. Below we discuss species and functional diversity patterns with elevation, as well as how area, MDE, climatic variables, EVI and Rapoport's elevational rule may influence the diversity patterns along the ridge of the Baekdudaegan.

3.1 Elevational diversity patterns

On the ridge of the Baekdudaegan, plant species richness and diversity exhibited hump-shaped patterns with elevation. The hump-shaped distribution in species diversity is the most commonly observed pattern in many taxa of various ecosystems [9]. At the most general level, our study adds to the growing body of evidence showing plant species diversity exhibits a strong hump-shaped pattern on mountains with changes in elevation, although the absolute elevations of the diversity peaks vary somewhat between studies. However, functional diversity based on Raunkiaer's life forms decreased with elevation in this study. Theory predicts that viable traits show a reduced variation as a result of ecological filtering along a gradient of environmental stress [46]. Furthermore, our results are consistent with those of a recent study showing a negative correlation in functional diversity of fruit size with elevation among the vascular plants in the Andean forests of the Ramal de Guaramacal [29]. However, we cannot guarantee that these linear patterns in elevational functional diversity are common because few studies exist related to the elevational patterns of functional diversity and because functional diversity generally depends on the functional traits and calculation methods used [27,29]. Therefore, the potential relationships between functional diversity and elevation open up a field for further research.

This study depicts different elevational patterns that exist between species and functional diversity, and the results also indicate that different components of biodiversity may vary independently of each other across environmental gradients. This implies that single indicators (i.e. species richness or diversity) could be incomplete surrogates of biodiversity and that the various components of biodiversity (i.e. functional diversity) have to be considered together [27]. Therefore, our study suggests traditional biodiversity indices have to be supplemented or replaced by functional diversity, which is used to measure those components of

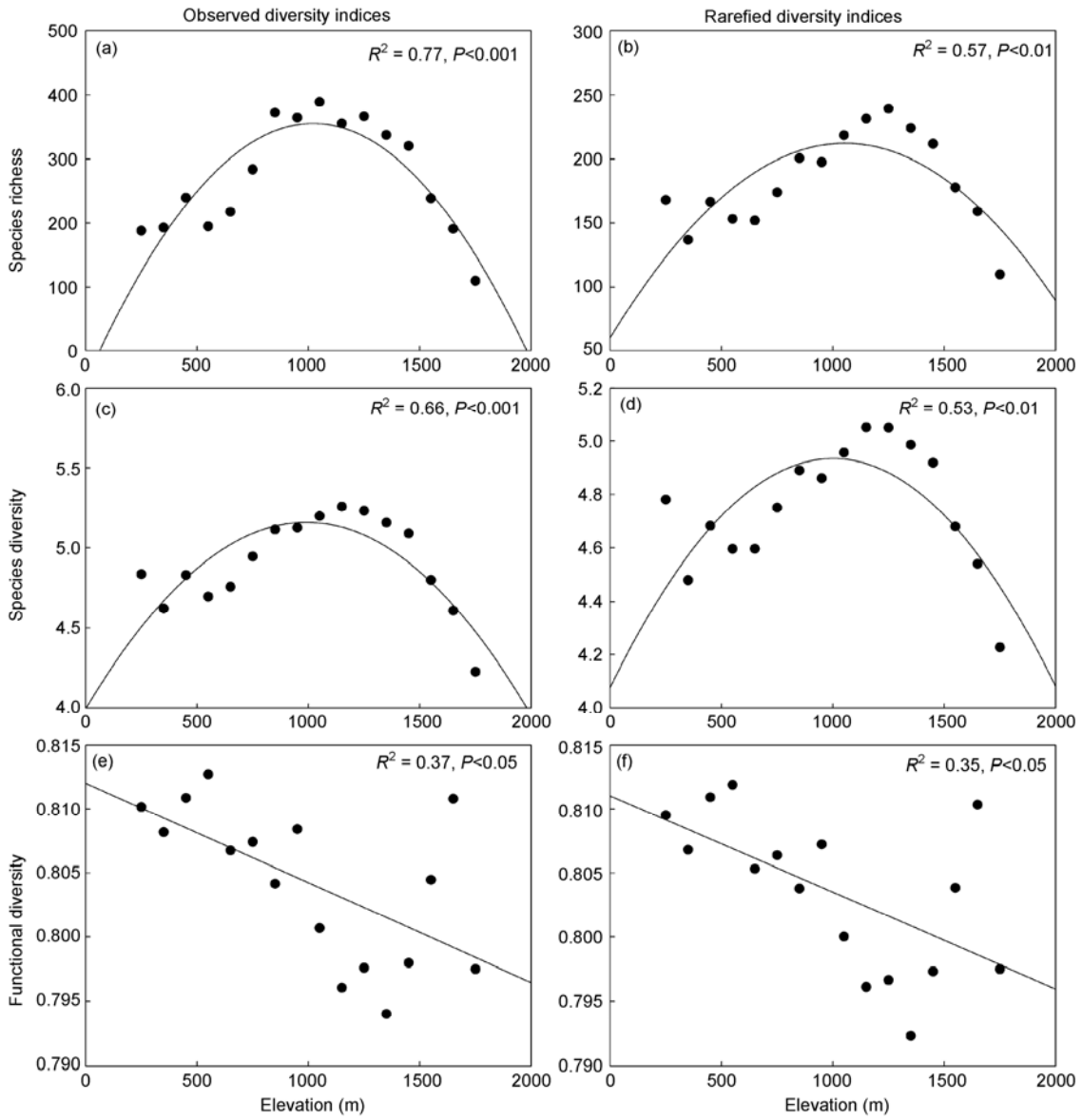

Figure 3 Relationships between elevation and species richness (a, b) and diversity (c, d) and functional diversity (e, f) along the ridge of the Baekdudaegan. All diversity indices were rarefied to rectify the bias caused by variations in sample size.

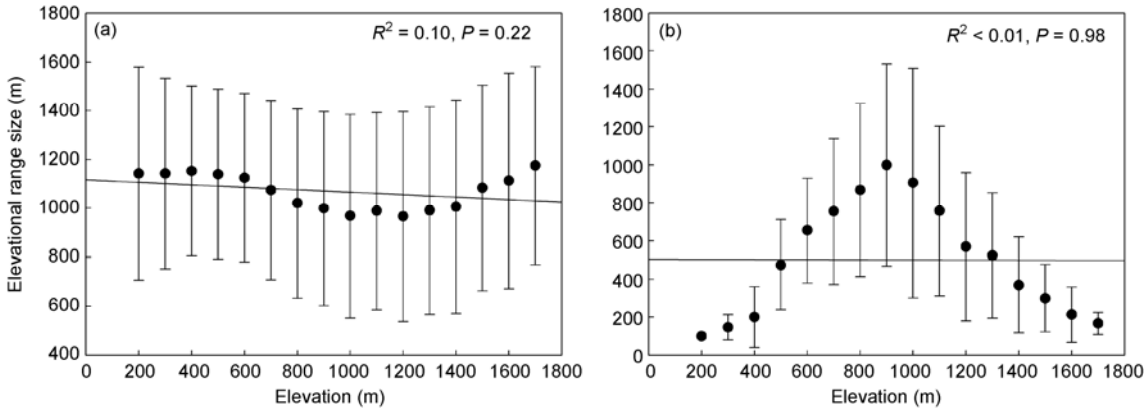

Figure 4 Relationships between elevation and elevational range size of plant species using (a) Stevens' and (b) midpoint methods to test Rapoport's elevational rule on the ridge of the Baekdudaegan.

Table 3 Forward stepwise multiple regression models for explained variables including all linear and quadratic terms and diversity indices along the ridge of the Baekdudaegan, South Korea

	Variables		Species richness		Species diversity		Functional diversity	
			Model A	Model B	Model A	Model B	Model A	Model B
Linear terms	Intercept	*t*	0.15^{ns}	8.49^{***}	23.93^{***}	53.53^{***}	22.82^{***}	22.82^{***}
	Area	*t*	(.)	5.09^{***}	(.)	3.63^{**}	(.)	(.)
	MDE	*t*	6.26^{***}	–	4.94^{***}	–	(.)	–
	MAT	*t*	(.)	(.)	(.)	(.)	3.71^{**}	3.71^{**}
	MAP	*t*	(.)	(.)	(.)	(.)	2.68^{*}	2.68^{*}
	EVI	*t*	(.)	(.)	(.)	(.)	(.)	(.)
		F	39.21	25.87	24.35	13.19	10.11	10.11
		R^2	0.74^{***}	0.65^{***}	0.64^{***}	0.49^{**}	0.61^{**}	0.61^{**}
Linear and quadratic terms	Intercept	*t*	4.15^{**}	8.49^{***}	41.84^{***}	53.53^{***}	35.72^{***}	35.72^{***}
	Area	*t*	(.)	5.09^{***}	(.)	3.63^{**}	(.)	(.)
	$Area^2$	*t*	(.)	(.)	(.)	(.)	(.)	(.)
	MDE	*t*	(.)	–	(.)	–	(.)	–
	MDE^2	*t*	6.95^{***}	–	5.23^{***}	–	(.)	–
	MAT	*t*	(.)	(.)	(.)	(.)	(.)	(.)
	MAT^2	*t*	(.)	(.)	(.)	(.)	3.61^{**}	3.61^{**}
	MAP	*t*	(.)	(.)	(.)	(.)	2.25^{*}	2.25^{*}
	MAP^2	*t*	(.)	(.)	(.)	(.)	(.)	(.)
	EVI	*t*	(.)	(.)	(.)	(.)	(.)	(.)
	EVI^2	*t*	(.)	(.)	(.)	(.)	(.)	(.)
		F	48.36	25.87	27.31	13.19	9.65	9.65
		R^2	0.78^{***}	0.65^{***}	0.66^{***}	0.49^{**}	0.60^{**}	0.60^{**}

a) Model A included all explanatory variables, while model B excluded the MDE. Magnitudes of *t*-values indicate the importance of each variable in the models. –, variable not included in model; (.), variable excluded from the stepwise multiple regression model; MDE, mid-domain effect; MAT, mean annual temperature; MAP, mean annual precipitation; EVI, enhanced vegetation index. ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

biodiversity that influence how an ecosystem operates or functions. Previous studies have also reported measures of species diversity do not consistently capture the functional differences among species that regulate ecosystem processes; therefore, functional diversity needs to be considered when developing species diversity indices [47]. Environmental filters might limit species composition to a given range of functional characteristics, thus limiting the degree of variation of functional diversity with respect to species diversity [48]. The increased species richness or diversity within a more homogenous pool of traits thus might lead to a finer division of the available niche space among similar species rather than to greater functional diversity. The degree of dependence of functional diversity on species diversity might be mostly related to the amplitude of the species' traits pool and on how species divide into the niche space available. This is a potential ground for understanding the mechanism that regulates the functioning of biodiversity under different environmental constraints [20].

3.2 Determinants of elevational diversity patterns

We observed a strong influence of spatial-related variables such as area and MDE on the elevational pattern of plant species richness and diversity in simple linear models, whereas climatic variables such as MAT and MAP also significantly contributed to observed patterns with area and MDE in quadratic models. In multiple regression models, only MDE was selected as the most powerful variable affecting species diversity patterns. Many studies have documented that the MDE was an important factor influencing species diversity patterns along elevational gradients [5,12,13]. The MDE is an abiotic and stochastic hypothesis, based on the premise that the spatial distribution of diversity is constrained by the shape of landmasses and by species' range size. Under these conditions, random placement of species ranges within a bounded domain creates an overlap of species ranges, and thus a peak of diversity, toward the center of the geographical domain [13]. However, we also found an interesting deviation from the MDE expectations of the null model (Figure 1(c)) despite the existence of a strong positive correlation between observed and predicted richness (Table 2). A recent work in the eastern Himalayas reported tree species richness largely deviated from that predicted by the MDE null model [5], as did species richness of other plant groups [12,49]. The large deviation may be a result of the presence of a large proportion of singletons and doubletons, which are species present in only one or two samples, respectively [49]. In this study, 36% of all plant species were represented by singletons and doubletons, and this high proportion of singletons and doubletons is likely to result in a large deviation. The degree of deviation

may also suggest that other factors (i.e., ecological, historical and evolutionary factors) could explain the observed distribution pattern [5]. Area was also an important predictor of plant species diversity pattern in simple regression models. However, area was a weak predictor of diversity patterns in multiple regression models with the MDE. This apparent contradiction is caused by the strong correlation between the MDE and area ($R^2 = 0.67$, $P < 0.001$) and the area effect is substituted by the MDE in the multiple regression models. Therefore, we suspect the effect of area was masked by the strength of the MDE, at least for the plant species diversity in this study. Although, climatic variables were excluded in the simple linear and multiple regression models, climatic variables might be also important for plant species diversity patterns. In fact, the best fit for these variables to the parabolic shapes of species richness and diversity was a quadratic function. If climatic variables contribute to observed patterns of species richness and diversity, it is likely that an optimal range of temperature and precipitation exists at intermediate elevations and that favorable climatic conditions at intermediate elevations may lead to higher plant species richness and diversity. The intermediate elevations may provide the best combinations of heat and water for plant growth and consequently allow a rate of higher resources use and the co-existence of more species [12].

When compared with species diversity indices, the MAT was a single most powerful factor for the functional diversity pattern in simple regression model on the ridge of the Baekdudaegan. In general, functional traits are considered to be a strategy plants use in response to the temperature gradient [25]. Moreover, the MAP was also an important factor in quadratic and multiple regression models. Climate is recognized as an obvious factor controlling species distribution and diversity in many areas, especially for vascular plants [50]. Many studies have revealed temperature and precipitation play a significant role in plant physiology, which in turn influences their distribution and diversity [51]. In this study, each functional trait used to calculate functional diversity showed different elevational patterns. Although geophytes and chamaephytes showed hump-shaped patterns and no relationship with elevation, respectively, most functional groups showed monotonically decreasing or increasing patterns. Two climatic variables are likely to contribute to the components of functional diversity with different ways: that is, temperature and precipitation may be more important for decreasing and increasing functional groups with elevation, respectively. Therefore, this study suggests that a combined interaction of temperature and precipitation may affect functional diversity patterns along the elevational gradient on the ridge of the Baekdudaegan.

Studies using remote sensing-based vegetation indices as surrogates of primary productivity have found significant productivity-diversity relationships, both linear and unimodal, suggesting that such estimates can be used to evaluate biodiversity patterns [6], albeit at different spatial scales depending on the taxonomic group in question [52]. This study finds little support for productivity (as measured by EVI) as a primary driver in shaping patterns of species and functional diversity along the elevational gradient. Although both functional diversity and productivity are linear with respect to elevation in this study, the distribution of productivity with elevation does not necessarily correspond with functional diversity for each elevational gradient. This suggests that the relationships between productivity and elevation and between productivity and diversity may be more complex than previously thought. Furthermore, poor support for productivity questions the energy-diversity hypothesis for vascular plants along an elevational gradient on the ridge of the Baekdudaegan. Recent studies suggest that energy input is only a strong predictor of diversity in the far northern portions of the globe, and that precipitation or the interaction between energy input and moisture shapes large-scale biodiversity patterns worldwide [51]. However, the results presented here provide weak support for this hypothesis as well, suggesting that the relationship between other explanatory variables and diversity along smaller spatial scales (i.e. a mountain range) may be incongruent with those found at larger spatial scales.

3.3 Rapoport's elevational rule

The results of this study do not support Rapoport's elevational rule (Figure 4). Because plant species along the ridge of the Baekdudaegan occurring the lowest and highest mean elevations tended to have smaller elevational ranges and because only species at intermediate elevations had large elevational ranges, an alternative and complementary explanation for the observed pattern seen is the random placement of species' elevational ranges along an elevational gradient, such as the MDE. Another possible explanation is the different patterns in the annual ranges of temperatures between various latitudinal and elevational gradients. Rapoport's rule is based on the fact that the annual range of temperature increases with latitude [53]. The rule was then extended to elevational gradients by Stevens [10], but without accounting for the presumption that the annual range of temperature increases with latitude. However, Tang and Fang [54] found that the annual range of temperature decreased (not increased as assumed by Stevens) with elevation by measuring temperature for one year along two elevational transects in Mt. Taibai, China. Their findings may explain why the Rapoport's rule is not very frequently observed to hold true along elevational gradients rather than latitudinal gradients. In any case, species ranges result from complex interactions among many factors, such as physiological traits, the complex evolutionary history of speciation and dispersal, and constraints resulting from continent shape [55]. No general trends appear to exist for Rapoport's elevational rule for all biological organisms, suggesting that

the factors determining range size are complex and remain poorly understood [56].

4 Conclusion

Along the ridge of the Baekdudaegan, plant species and functional diversity showed different elevational patterns. Plant species diversity had distinctly hump-shaped patterns along the elevational gradient, even though the absolute elevations of the peaks were somewhat different between species richness and diversity. However, functional diversity decreased monotonically with elevation. The MDE was the most important explanatory variable for species richness and diversity patterns, whereas the climatic variables were important predictors for functional diversity pattern. Furthermore, Rapoport's elevational rule was not supported for terrestrial plants at least along the ridge of the Baekdudaegan. This study suggests the following: (1) Traditional biodiversity indices such as species richness and diversity have to be supplemented or replaced by functional diversity, which is used to measure those components of biodiversity that influence how an ecosystem operates or functions; (2) different elevational patterns may be observed among different diversity indices even in the same taxon, and there may be fundamental differences in the mechanisms underlying these diversity patterns; therefore, (3) further study including other the inclusion of variables, such as habit heterogeneity, human disturbance and evolutionary history as well as spatial, climatic and energy-related variables at different spatial scales with a combination of species and functional diversity complementing each other, should be consistently evaluated to achieve a better understanding of the elevational patterns of plant communities in mountain ecosystems.

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Supporting Information

Table S1 Frequencies of plant species found at each elevational band along the ridge of the Baekdudaegan Mountains

The supporting information is available online at csb.scichina.com and www.springerlink.com. The supporting materials are published as submitted, without typesetting or editing. The responsibility for scientific accuracy and content remains entirely with the authors.